PREDATORY INTERACTIONS BETWEEN MUD-DAUBER WASPS (HYMENOPTERA, SPHECIDAE) AND *ARGIOPE* (ARANEAE, ARANEIDAE) IN CAPTIVITY

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ABSTRACT. We report on efforts to maintain two common sphecid wasps, *Chalybion caeruleum* (Saussure 1867) and *Sceliphron caementarium* (Drury 1773), in field and laboratory enclosures in order to observe their predatory interactions with the orb-weaving spiders *Argiope aurantia* Lucas 1833 and *A. trifasciata* (Forskål 1775). Both species of wasps seemed to locate webs primarily by chance while flying along the tops of the vegetation but differed greatly in their hunting tactics once webs were located. *Sceliphron caementarium* was most successful at capturing spiders that had dropped out of webs in response to the wasp's hitting the web. But, *C. caeruleum* often employed a type of aggressive mimicry: it landed in the web or used its middle legs to pluck the web, luring the spider to the wasp. *Argiope* did not differ in their defensive response to *C. caeruleum* and *S. caementarium*. Most *Argiope* dropped out of webs in response to attacks rather than using other defensive behaviors such as shuttling between sides of webs or vibrating webs.

Keywords: Sympatry, competition, niche partitioning

Sphecid wasps are common predators of orb-weaving spiders. Because individual wasps capture several spiders to provision each cell in a nest and build multiple cells over their lives (Coville 1987), mud-dauber wasps can act as a particularly potent selective force on the evolution of spider defensive behaviors. Many studies have examined the numbers and species of spiders provisioned in wasp nests, providing insight into which spiders may be most vulnerable to wasps (e.g., Muma & Jeffers 1945 and references in Krombein et al. 1979). These studies indicate that different species of wasps that hunt in the same habitat, such as *Chalybion caeruleum* and *Sceliphron caementarium*, often catch different prey. This suggests that sympatric species of sphecids may employ different predatory tactics, perhaps due to niche partitioning. There are few, mostly anecdotal, observations on the hunting tactics of sphecids (Peckham & Peckham 1905; Rau 1928, 1935; Eberhard 1970; Endo 1976; Coville 1987; Rayor 1997). But, there has been no comparative study of the hunting behaviors of sympatric *C. caeruleum* and *S. caementarium*.

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Little is known about the primary and secondary defensive behaviors orb-web spiders use against sphecids. Yet, it is the interaction of spider defensive behaviors and the predatory tactics of wasps that determine if individual spiders survive predation attempts (Cloudsley-Thompson 1995; Edmunds & Edmunds 1986; Tolbert 1975). There are two detailed studies of wasp-spider interactions, but these focus on wasps hunting nocturnal or colonial orb-weaving spiders (Eberhard 1970; Rayor 1997). What is missing, therefore, are studies of the interactions of wasps with solitary, diurnal spiders, such as *Argiope*.

Argiope is among the most intensively studied genera of spiders and is likely to be particularly vulnerable to visually-hunting predators because it rests at the center of its web during daylight. *Argiope* is also an important model for testing hypotheses concerning possible defensive functions of structures such as barrier webs (Higgins 1992) or stabilimenta (Blackledge & Wenzel 1999). Here we report on our efforts to maintain two species of sphecid wasps (*C. caeruleum* and *S. caementarium*) in field and laboratory enclosures and our observations of their predatory interactions with the orb-weaving spiders *Argiope aurantia* and *A. trifasciata*.

METHODS

We observed the hunting behaviors of *C. caeruleum* and *S. caementarium* in one indoor enclosure (1998 and 1999) and three outdoor enclosures (1999). All wasps were collected as adults in the field (Dublin, Ohio), except for a single *C. caeruleum* that emerged from a previously collected nest during the 1998 study. The collection site consisted of old barns surrounded by old fields. The primary prey caught by wasps at this site were immature *A. trifasciata* (pers. obs.). Individual wasps were distinguished by paint on the thorax or abdomen.

The 3.4 × 2.7 × 2.2 m screened indoor enclosure was located in Ohio State University's Insectary, Columbus, Ohio, in a greenhouse room with light and temperature maintained near outdoor levels. Assorted plants, including flowering *Echinacea* (Asteraceae) and *Lantana* (Verbenaceae), were scattered throughout the enclosure to provide resting places for wasps. The plants also simulated the natural background of foliage in which wasps hunt spiders, a potentially important feature of the study because background may influence the conspicuousness of spider silks to insects (Blackledge 1998a; Blackledge & Wenzel 2000). A 20 × 30 cm plastic pan was placed in one corner of the enclosure and contained a layer of earth from the same pond at the field site where wild *S. caementarium* collected mud for their nests. The pan was partially filled with water and then tilted to create a moisture gradient from completely saturated to nearly dry, simulating the bank of the pond. Mud nests of *S. caementarium*, collected at the field site, were glued to wooden boards in the upper corners of the enclosure to encourage building of new nest cells by *S. caementarium*. These nests also provided vacant cells for *C. caeruleum*, which nests only in abandoned *S. caementarium* cells (Rau 1928). In 1998, petri dishes containing a sucrose and honey mixture were placed on the floor of the cage to provide wasps with a nectar source. In 1999, a plastic hummingbird feeder filled with a 1:1 honey:water solution was used instead. The honey water was changed every two days to prevent fermentation.

The three outdoor enclosures consisted of nylon screening over wood frames (3.8 × 2.3 × 2.0 m) and were located in a field at Ohio State University's Rothenbuhler Honeybee Laboratory, Columbus, Ohio. We found it necessary to cover the bottom edge of the screening with thick layers of bark mulch and stone to prevent wasps from crawling under the edges of the enclosures. The natural ground cover consisted of various grasses (Poaceae) and thistle (Asteraceae), with a thick layer of thatch. There were some naturally occurring *A. trifasciata* in the surrounding field. Again, each enclosure had a 20 × 30 cm plastic pan containing mud and water, wooden boards with mud *S. caementarium* nests glued to them, and a hummingbird feeder as a nectar source.

Immature *A. aurantia* and *A. trifasciata* were collected from roadside ditches in and around Columbus. Most of the spiders were uniquely marked and weighed immediately after collection. Spiders were allowed to build their webs in 35 × 35 × 10 cm wooden frames as described in Blackledge (1998b) but modified with both plastic sides being removable. We placed individual frames containing spiders within the enclosures to observe wasp-spider interactions. We recorded our observations on audio tape and also video-taped a few of the encounters. We also include some observations on *A. trifasciata*, in webs on natural plant supports, which we placed in the same outdoor enclosures and one of us (TAB) used for a second study examining the role of stabilimenta as wasp defenses. We released a variety of araneid, linyphiid and tetragnathid spiders into the indoor enclosure to provide alternative prey, while the outdoor enclosures naturally contained a variety of agelenids, salticids and thomisids as well as *Cyclosa conica* (Pallas 1772) and *Uloborus glomosus* (Walckenaer 1841). Because we later found few individuals of these species in wasp nests (10 of 142 excavated spiders) and we never directly observed a predation event involving these species, we exclude them from further discussion.

RESULTS

In the indoor enclosure, we observed 24 attempted predation events during 20 days of observation (between 4–28 August 1998 and between 28 July–17 August 1999). In the outdoor enclosures, we observed 50 predation attempts during observations every day between 21 August and 11 September 1999. *Chalybion*

Table 1.—Predatory tactics of two species of sphecid wasp, *C. caeruleum* and *S. caementarium,* and the common defensive responses by immature *A. aurantia* and *A. trifasciata.* Observations were made on 3 individuals of *C. caeruleum* and 5 individuals of *S. caementarium.* The heading "Spider approached wasp" includes approaches by spiders to either wasps landing in webs or plucking webs. Defensive responses of spiders were not mutually exclusive. Asterisks denote significant differences, using binomial probability, between species of wasps in frequency of behaviors (*$P < 0.05$, **$P < 0.01$, ***$P < 0.005$).

	C. caeruleum	*S. caementarium*
Observed attacks	48	26
Location of capture:		
web center	6	3
capture zone or frame threads	14	6*
ground below web	4	11**
Total	24	20
Wasp landed in web	22	3***
Wasp plucked web	11	0**
Spider approached wasp	15	1**
Response of spider:		
drop from web	21	15
abandon web	7	7
move to web periphery	15	6
Mass of spiders captured:		
mean ± standard deviation	0.04±0.01 mg	0.04±0.02 mg
range	0.02−0.07 mg	0.02−0.08 mg

caeruleum opened their nests and began hunting between 1000–1200 h and resealed their nests between 1400–1700 h or, if no spiders were captured, after only 30 min. *Sceliphron caementarium* typically opened nests for the entire day (1000–1700 h). Like other sphecids, both *C. caeruleum* and *S. caementarium* often did not hunt on overcast, rainy days and became active much later than normal on cooler days (see also Freeman & Johnston 1978; Powell 1967). Encounters were sometimes brief—lasting only a few seconds if spiders were caught at the centers of webs, and sometimes much longer, lasting 2–3 min if spiders attempted to escape by dropping and then moving rapidly through the grass. We combined all of the data for each species of wasp (Table 1) and, within each species, we had approximately the same number of observations for each individual wasp. We only included observations on predation attempts on spiders that were within the size range captured by wasps during the experiment (Table 1).

Both wasp species seemed to locate webs by chance while flying along the top of the vegetation in a seemingly haphazard flight path. However, *S. caementarium* and *C. caeruleum* differed greatly in their hunting tactics once webs were located (Table 1). *Sceliphron caementarium* bumped into webs while flying, but then flew off without seeming to react to webs as anything other than physical barriers. But, these wasps vigorously pursued spiders that dropped from webs, spending as much as 2–3 min crawling around the thatch and grass stems under webs in gradually enlarging circular patterns until either spiders were located or wasps began flying again.

In contrast *C. caeruleum* often landed in webs or on the substrate supporting webs and then used their middle legs to pluck the silk. When in a web, *C. caeruleum* sometimes contracted its entire body every few seconds for up to two minutes. In 68% of these instances, spiders ran to wasps after wasps had landed in or plucked at webs. Many of these spiders (70%) were caught as they approached wasps or as wasps chased them back to the centers of webs, but others immediately dropped out of webs upon contacting wasps.

Captured spiders were stung between the carapace and sternum in the posterior of the cephalothorax. Paralysis appeared to be in-

stantaneous, but spiders were occasionally stung multiple times, stings lasting up to a few seconds. Wasps carried spiders by holding the pedipalps in their mandibles, with the venters of spiders facing toward the venters of wasps. Wasps commonly pressed their mandibles against the chelicerae of spiders for a few seconds after capture, perhaps drinking hemolymph. After about 25% of captures, both species of wasp drank hemolymph from the chelicerae or coxae of spiders for periods of up to 1 min. Four of those spiders were subsequently discarded instead of being used to provision a nest.

We observed 9 instances (not in Table 1) where a wasp attacked a spider, grasped the spider with its legs, wrapped its abdomen around the spider as though stinging it, but then released the spider and flew away. In each instance the spider was still alive and ran away when touched by one of us. All but two of those spiders weighed within the mean ±2 standard deviations of *Argiope* captured during the study.

DISCUSSION

Eberhard (1970) concluded that contrast between a spider and the background upon which it rested was one of the most important cues used by *S. caementarium* to locate *Larinioides* (*Araneus*) *cornutus* (Clerk 1757), which were hiding in retreats near webs. In our study, both *C. caeruleum* and *S. caementarium* often alighted upon dark spots of debris or the shadows of insects or spiders on the opposite side of the screen tent, which supports Eberhard's hypothesis that wasps respond to contrast. However, *S. caementarium* attacked very few spiders at the centers of webs, instead seeming to stumble into and out of webs without regard for the possible presence of spiders. *Ccalybion caeruleum* and *S. caementarium* often flew within 2 cm of spiders on webs or grass, without reacting to the spiders, but quickly chased spiders once spiders dropped from or moved within webs. Both of these observations suggest that contrast was not actually used to locate *Argiope* in our study. There are at least two potential explanations for this difference with Eberhard's findings. The light-colored bodies of juvenile *Argiope* may reflect significant UV light (Craig & Ebert 1994), and this may provide a poor contrast against natural back-

grounds to insects, much as stabilimentum silk can (Blackledge 1998a; Blackledge & Wenzel 2000). Another possible explanation is that motion may be an important cue in eliciting attacks by *S. caementarium*. This second explanation seems particularly likely because *S. caementarium* pounced on small moving insects or even falling debris, particularly when wasps were searching for spiders flushed from webs.

Sceliphron caementarium aggressively pursued spiders that dropped from webs, catching most prey by chasing spiders on the ground, while *C. caeruleum* used aggressive mimicry to catch spiders that were still in webs (Table 1). *Chalybion caeruleum* landed in webs and then plucked at the silk in webs, luring spiders to themselves. In almost 70% of encounters where *C. caeruleum* landed in or plucked webs, spiders approached wasps; and most of those spiders were captured with little chase. We even observed one instance where a spider, which had dropped out of its web into the grass, proceeded to crawl back up its dragline to the web center and then to a *C. caeruleum* as the wasp plucked the web. This plucking behavior is similar to that described for *Chalybion* spp. (Schwarz, in Howard 1901; Coville 1976) and *Trypoxylon* sp. (Rau 1926; pers. obs.) and may be a particularly effective method to hunt retreat dwelling spiders (Coville 1976). One vespid is also thought to use vibrations caused by tapping with its antennae to lure spiders to the hubs of webs (MacNulty 1961).

Sceliphron caementarium nests contain a wider range of spider prey than the nests of *C. caeruleum*. *Sceliphron caementarium* provisions nests with both web-building and cursorial spiders, while the nest contents of *C. caeruleum* are largely restricted to orb and tangle web-building spiders (Krombein et al. 1979; Muma & Jeffers 1945). These differences in nest provisioning likely reflect the different hunting tactics used by these two species of wasps. The use of old *Sceliphron* nests by *Chalybion* (Rau 1928) restricts *Chalybion* to hunting in habitats occupied by *Sceliphron*. Thus, competition has likely been an important selective factor in the evolution of *Chalybion* and *Sceliphron* hunting behaviors. Therefore, the specialization on web-building spiders by *Chalybion* could be due to niche partitioning.

Argiope used similar defensive behaviors against both species of wasps (Table 1). The most common response to attacks was for spiders to drop from webs (50% of encounters) and then either freeze or run to nearby cover. Spiders often maintained contact with their webs via draglines and returned 2–10 min later. But, spiders sometimes abandoned webs completely, moving up to 1 m away, in deep grass. *Argiope trifasciata* on natural webs built in the grassy outdoor enclosures also sometimes abandoned webs when attacked. They would then build webs in new locations the next day, without having consumed the abandoned web. These observations suggest that field researchers should use caution when assuming that abandoned webs always indicate predation, because abandoning webs is itself a defensive strategy.

Occasionally a spider ran to the top or side of its web (30% of encounters), remaining motionless for up to several minutes before returning to the web center. Spiders that remained at web hubs often stilted, holding their bodies far out from webs and angling their abdomens away from the plane of webs. We suggest that these defensive behaviors might be relatively specialized responses to wasp predators (see also Cushing & Opell 1990), because spiders did not engage in other common defensive behaviors such as web flexing or shuttling (Cloudsley-Thompson 1995; Edmunds & Edmunds 1986; Tolbert 1975). Web flexing is often initiated when humans approach webs (pers. obs.) and may function against salticid predators (Tolbert 1975) but was never used against wasps. While our observations supplement descriptive works on the behavioral interactions of wasps and spiders, we hope that the use of enclosures will also facilitate a more experimentally-based approach to the study of wasp-spider interactions.

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